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RESEARCH ARTICLE

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Functional biogeography of marine vertebrates in Atlantic Ocean reefs

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Abstract

Aim: Marine vertebrates play key functional roles on reef ecosystems. Despite their phylogenetic distance, different vertebrate lineages could play similar functions on reefs, which has been overlooked by current research on marine functional biogeography. We provide the first comprehensive assessment of the functional structure and inventory of ecosystem functions delivered by 224 vertebrates—marine mammals, sea turtles, sharks, rays and bony fish—in Atlantic Ocean reefs.

Location: Atlantic Ocean reefs.

Methods: We compiled six species-level traits and investigated geographical patterns of functional richness (FRic), functional uniqueness (FUn) and specialization (FSpe) in 83 assemblages. Additionally, we simulate the effects of marine vertebrate species' extinction on functional diversity metrics.

Results: Sharks, rays and bony fish species had the highest overlap in functional space (30.94%), while turtles overlapped mainly with bony fishes (1.76%). The functional structure of vertebrate assemblages is not homogeneous across the Atlantic. While functional richness peaks in the Caribbean (a "*functional hotspot*"), this region depicts low-to-intermediate functional uniqueness and functional specialization levels. Despite the large proportion of threatened top predator species (53.1%), mainly large-bodied sharks, it is the loss of mesopredator species that will severely impact (up to 94% of functional loss) the functional space of vertebrate assemblages in Atlantic Ocean reefs.

Main conclusions: Our study reveals that functional richness patterns of vertebrate assemblages differ across Atlantic Ocean reefs. Despite the low values of functional uniqueness and specialization in some reef assemblages, reef functioning can still be compromised due to species' extinctions. The impact of mesopredators' loss over the functional structure of vertebrate assemblages is worrisome since this group holds a considerable proportion of threatened species (20.1%) and is next in line considering the anthropogenic impacts over high trophic level species.

Mariana Bender and Fabien Leprieur share the co-senior authorship

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KEYWORDS
coral reefs, cross-taxa, ecosystem functions, marine megafauna, multi-taxa, threatened species

1 | INTRODUCTION

Human influence has reached almost every place on Earth (Lewis & Maslin, 2015; Steffen, Crutzen, & McNeill, 2007). In the oceans, intense and widespread anthropogenic impacts such as overfishing, pollution and habitat loss are threatening species and their functions (He & Silliman, 2019; Young et al., 2016). Marine biodiversity has been declining and changing considerably over the Anthropocene, with potentially greater losses of top predators (e.g. mainly sharks), large-bodied (e.g. marine megafauna), habitat specialists and species with terrestrial contact (e.g. sea turtles and pinnipeds; Ceretta et al., 2020; McCauley et al., 2015; Pimiento, Leprieur, et al., 2020). Nevertheless, the influence of declines and changes in biodiversity on ecosystem functions such as productivity, nutrient cycling and trophic regulation still needs to be better understood (Bellwood et al., 2019; Fonseca & Ganade, 2001; Larsen et al., 2005; Levine, 2016; Mouillot et al., 2014). Within that context, the use of functional diversity can reveal the effects of biodiversity loss on ecosystem functioning, beyond the loss of taxonomic entities (Bellwood et al., 2004; Mouillot et al., 2014; Pimiento, Leprieur, et al., 2020; Tavares et al., 2019; Villéger et al., 2017). Our study aims to identify the potential overlap in functions of vertebrate species from distant lineages and assess the effect of simulated species loss on reef ecosystem functions.

The extinction of reef fauna has largely contributed to the declines and changes in species and functions observed in the oceans (Bellwood et al., 2004; Hammerschlag et al., 2019; Heithaus et al., 2008; Pimiento, Leprieur, et al., 2020). Top predators such as sharks consume large amounts of prey body mass and control their populations (Ruppert et al., 2013). Grazers, in their turn, can limit algae growing and ensure coral reef resilience (Adam et al., 2015; Christianen et al., 2019; Goatley et al., 2012). Species traits are assumed to be linked to these ecological functions (e.g. maximum body size, body mass, trophic group, schooling behaviour, metabolic rate and mobility; Bellwood et al., 2019; Tavares et al., 2019). The role of top predators is linked to high trophic levels, large body sizes and body mass (Roff et al., 2016; Tavares et al., 2019), while effective grazing appears related to eye diameter and position, gape position and shape, total gut length and body size (Bonaldo et al., 2014; Villéger et al., 2017). A single trait as body size, for example, is related to bioturbation (Bonaldo et al., 2014; Tavares et al., 2019), individual mobility (Villéger et al., 2017), nutrient cycling (Allgeier et al., 2014; Tavares et al., 2019), trophic regulation and community structuring in marine vertebrates (Tavares et al., 2019). Yet, the diversity of ecosystem functions performed by different taxonomic groups and their degree of functional redundancy in reef assemblages remains poorly known.

When ecological communities lose species, they do not necessarily lose functions and services (Mouillot et al., 2014) because these can be insured by species with similar traits relative to the species being lost (Mouillot et al., 2014; Pimiento, Bacon, et al., 2020). Such "functional redundancy" is an emergent property of ecological communities that depends on local species richness and trait similarity among co-occurring species—more species implies more functions, and more species per function implies more insurance (Fonseca & Ganade, 2001; Halpern & Floeter, 2008; Pimiento, Leprieur, et al., 2020; Rosenfeld, 2002). Also, functions and services may be insured by distantly related taxa (e.g. algae removal may be maintained by fishes after sea turtles become locally extinct; Goatley et al., 2012); however, we have just an incipient knowledge about functional redundancy across taxa (e.g. Pimiento, Leprieur, et al., 2020). For example, "functional uniqueness," which is an indicator of functional redundancy according to the overall isolation of each species in total trait space, highlights the irreplaceability of each species to perform unique ecosystem functions and services (Bellwood et al., 2003; Mouillot, Bellwood, et al., 2013; Pimiento, Leprieur, et al., 2020); the extinction of functionally unique species implies direct loss of such ecosystem properties (Mouillot et al., 2014). "Functional specialization" represents the mean distance of a species from the total species pool in trait space, with specialist species exhibiting extreme trait combinations, and contributing for functional diversity (Griffin et al., 2020; Mouillot et al., 2013).

Here, we provide a comprehensive assessment of the functional diversity of reef vertebrates from the Atlantic Ocean, including the Caribbean Sea. First, we compiled a taxonomically comprehensive database of the ecosystem functions of 224 species of bony fishes, sharks, rays, sea turtles and mammals. Traits compiled were maximum body size, maximum body mass, trophic group (diet), maximum depth, caudal fin and body shape classifications and are linked to six reef species functions: herbivory pressure, bioturbation/bioerosion, coral reef resilience, mesopredation, top predation and trophic regulation (Bellwood et al., 2019; Tavares et al., 2019; Villéger et al., 2017). Then, we spatialized such trait information at the regional and local assemblage levels to provide a geographically comprehensive assessment of the influence of marine vertebrate loss on Atlantic Ocean reefs. We simulated future extinction scenarios of vertebrate species extinction based on IUCN ranks and quantified the impact of potential species losses on functional diversity in Atlantic reefs (Leitão et al., 2016). If species richness safeguards functions,

then future extinctions in species-rich regions should not influence functional richness. In contrast, future extinctions should erode functional richness and redundancy in species-poor areas, but should increase the uniqueness between closest species. Additionally, we tested the hypothesis that the future extinction of sharks should cause decreases in community functional richness due to its combinations of functional traits (e.g. large size, body mass and trophic group) and importance in the regulation of trophic cascades. In this case, the ecosystem functions performed by this group, as that of top predators, should be under greater threat (Dulvy et al., 2014; Heithaus et al., 2008). Also, we predicted that herbivory would be severely compromised at local reef communities (Atwood et al., 2020; Bellwood et al., 2004), due to the low number of species that support this function in Atlantic Ocean reefs (Siqueira et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Database

We compiled information on 224 marine vertebrate reef-associated species: four marine mammals, five sea turtles, 89 elasmobranchs and 126 bony fishes. The species considered here use rhodolith beds, coral and rocky reefs or coralline algae banks for sheltering, feeding and spawning (Pinheiro et al., 2018). The Teleostei families considered were Acanthuridae, Carangidae, Epinephelidae, Kyphosidae, Lutjanidae, Girellidae, Serranidae subfamily Epinephelinae and the Labridae subfamily Scarinae (parrotfishes), based on the recognized importance of these groups as predators, mesopredators or herbivores in reefs (Bonaldo et al., 2014; Ferreira & Gonçalves, 2006; Longo et al., 2014; Morais et al., 2017). The list of Atlantic reef fish species was obtained by combining (1) the most up-to-date available inventory of Elasmobranchii and Teleostei for the Southwestern Atlantic region (Pinheiro et al., 2018) with (2) the GASPAR Project database (General Approach to Species-Abundance Relationships) that provided data for Teleostei species found in the Atlantic Ocean (Bender et al., 2017; Kulbicki et al., 2013; Parravicini et al., 2013) and (3) the International Union for Conservation of Nature occurrence data for Elasmobranchii species of the Eastern Atlantic (IUCN, 2019). Sea turtles and marine mammal species associated with reef environments in the Atlantic were compiled from the available literature (IUCN, 2019; Palomares and Pauly, 2019). For these four groups, shapefiles of species distributions were downloaded from the IUCN website (IUCN, 2019). A complete list of bony fish, sharks, rays, mammals and sea turtle families and species included in our research is available at Table S1.

To build a species presence matrix at the Atlantic Ocean scale and to capture regional variation on reefs' structure and diversity, we divided the Atlantic reef area into ten provinces (sensu Spalding et al., 2007): Warm Temperate Northwest Atlantic, Tropical Northwestern Atlantic, North Brazil Shelf, Tropical Southwestern Atlantic, Warm Temperate Southwestern Atlantic, St Helena and Ascension Islands, Benguela, Gulf of Guinea, West African Transition and Lusitanian. Then, we extracted species presence–absence data for each province and built a 4 × 4-degree grid (~440 km) over species distributions on Atlantic reefs because several species in our data set have a broad geographical distribution. In total, 83 grid cells were mapped into the Atlantic Ocean provinces, with each grid cell representing a vertebrate reef assemblage.

2.2 | Species traits and ecosystem functions

We compiled traits that represent species performance and fitness in reef environments, as well as a consistent link with ecosystem functions (Pimiento, Leprieur, et al., 2020; Tavares et al., 2019; Villéger et al., 2017). Traits assigned to species in this study were maximum body size (cm), maximum depth of occurrence, trophic group (diet category), maximum body mass (g), caudal fin morphology and body shape classifications (Table 1). Trait data were compiled from FishBase (www.fishbase.org), SeaLifeBase (www.sealifebase.org), IUCN (www.iucnredlist.org), and also from a literature search. For Teleostei reef fish species, maximum body size (cm), inhabited depth category (maximum depth of occurrence) and trophic group (diet category) traits were obtained from the GASPAR Project database (Mouillot et al., 2014) and from the most up-to-date list of traits for Atlantic reef fishes (Quimbayo et al., 2021). Maximum body mass **(M)** was estimated for each species using weight–length relationships: $M = aLt^b$, where **Lt** is the species' maximum recorded length and **a** and **b** were coefficient estimates for species, which were obtained from FishBase and SeaLifeBase references (Froese & Pauly, 2019; Palomares & Pauly, 2019). For species lacking specific length–weight parameters, we used averaged congener coefficients. The depth categories followed an ascending depth order (Pinheiro et al., 2018). Marine mammals actually have tails, but we classified them as caudal fins so that this attribute would be comparable across different taxonomic groups. This classification was extended from bony fish species (Quimbayo et al., 2021) and applied cross-taxa because the caudal fin determines swimming capacity/ability and prey capture efficiency (Fish et al., 2008; Fu et al., 2016; Lingham-Soliar, 2005; Villéger et al., 2017), and is therefore associated with functions based on vertebrate species feeding and position in the water column. For species without caudal fin, as turtles and 20 ray species, "absent" was inserted for that trait.

Ecosystem functions of each reef vertebrate species were compiled from the literature through an online search using the following keyword combinations: "spp. + ecosystem function" and "spp. + ecosystem functioning." These functions were then categorized based on Villéger et al. (2017) and Tavares et al. (2019): "ecosystem engineering," "participating to nutrient cycles" and "controlling food webs." The first study presents a classification for the main ecosystem functions associated with bony fish species—food web control, ecosystem engineering, and contribution to nutrient cycling—and served as the basis for our categorization of ecosystem functions.

TABLE 1 Functional traits and their relationship with ecosystem functions performed by 201 marine vertebrate species of distinct taxonomic groups in Atlantic Ocean reefs, assessed in this study

Functional trait	Ecosystem function	Nature	Modalities	References
Maximum body size	Food acquisition; nutrient transport and storage; capacity to connect disparate ecosystems	Continuous	Maximum body size in centimetres	Froese and Pauly (2019), Palomares and Pauly (2019), IUCN (2019), Mouillot et al. (2014)
Maximum body mass	Metabolic demand; food acquisition; nutrient transport and storage; per capita excretion rates	Continuous	Body mass in grams	Froese and Pauly (2019), Palomares and Pauly (2019)
Maximum depth	Habitat use; location of ecosystem contributions; nutrient transport and storage; trophic–dynamic regulation	Ordinal	Shallow (<30 m), medium-depth (30–50 m), deep (50–100 m) and very deep (>100 m)	Froese and Pauly (2019), Palomares and Pauly (2019), IUCN (2019), Mouillot et al. (2014)
Trophic group	Controlling food webs; nutrient transport and storage; capacity to partition the niche; capacity to provide trophic functional redundancy	Categorical	Carnivores, piscivores, planktivores, mobile invertebrate feeders, omnivores, herbivores, scraper herbivores, excavator herbivores, browser herbivores and algal feeders	Bonaldo et al. (2014), Ferreira et al. (2004), Longo et al. (2014), Pimiento, Leprieur, et al. (2020), Tavares et al. (2019)
Caudal fin	Mobility within/between habitat(s)	Categorical	Forked, heterocercal, lanceolated, lunated, rounded and truncated	Compagno et al. (2005), Last et al. (2016), Quimbayo et al. (2021)
Body shape	Mobility within/between habitat(s); social interactions	Categorical	Circular, short deep, wedge shaped, elongated, rhombic, fusiform, oval, diamond-shaped, eel like and shovel shaped	Compagno et al. (2005), Last et al. (2016), Quimbayo et al. (2021)

Note: The set of trait and ecosystem functions was based in refs. Pimiento, Leprieur, et al. (2020), Tavares et al. (2019) and Villéger et al. (2017).

Tavares et al. (2019) present a compilation of marine megafauna traits associated with ecosystem functions and services.

2.3 | Data analysis

Analysis of the functional structure of Atlantic reef vertebrate assemblages was conducted at four spatial scales: (1) regional scale, which corresponds to the Atlantic Ocean; (2) province scale, where we explored the functional richness of vertebrates in 10 provinces (sensu Spalding et al., 2007); (3) three distinct marine regions, namely the Caribbean, the Southwestern Atlantic and Eastern Atlantic and (4) the assemblage scale, represented by 83 grid cells. At each of these scales, we calculated species richness, functional indices, namely functional richness (FRic), functional uniqueness (FUn) and functional specialization (FSpe), and the effect of species loss over the functional structure.

2.3.1 | Functional diversity at the Atlantic reef space

To assess the functional diversity of Atlantic reef vertebrates at the regional and province scales, quantitative traits as species' maximum body size (cm) and maximum body mass (g) were first standardized to avoid that traits with large variation cause a disproportional influence on results (*scale* function; "base" Package; R Core Team, 2018). We then measured the dissimilarity across the 224 species in our data set considering their six functional traits using the Gower distance (Gower & Legendre, 1986) and conducted a Principal Coordinate Analysis (PCoA) to ordinate species into a functional space (Villéger et al., 2008). To assess the quality of the functional space, we used the mean squared deviation (mSD; Maire et al., 2015) (Figure S1). According to this metric (mSD), we selected the four main PCoA axes to build the functional trait space because a 4D space faithfully represents the original Gower's distances. The functional spaces occupied by vertebrate assemblages in Atlantic Ocean reefs, by different taxonomic groups and by threatened and non-threatened species were calculated using the *convhulln* function ("geometry" Package) (Habel et al., 2015). We also applied this function to measure the overlap between different taxonomic groups in functional space. To assess the unique and shared functions of reef vertebrate fauna, we grouped species according to their ecosystem functions categories (see Figure 1) and linked the position of these species in functional space using the *ordiellipse* function (VEGAN Package; Oksanen et al., 2018). Finally, we used Redundancy Analysis (RDA) (VEGAN Package) to summarize the variation in ecosystem functions (response variables) that can be explained by species traits—that is which traits are associated with the ecosystem functions performed by reef vertebrate species. We performed an ANOVA using functional traits as fixed factors and ecosystem functions as the dependent variable and assessed the relationship between traits and ecosystem functions summarized by the RDA ("stats" Package).

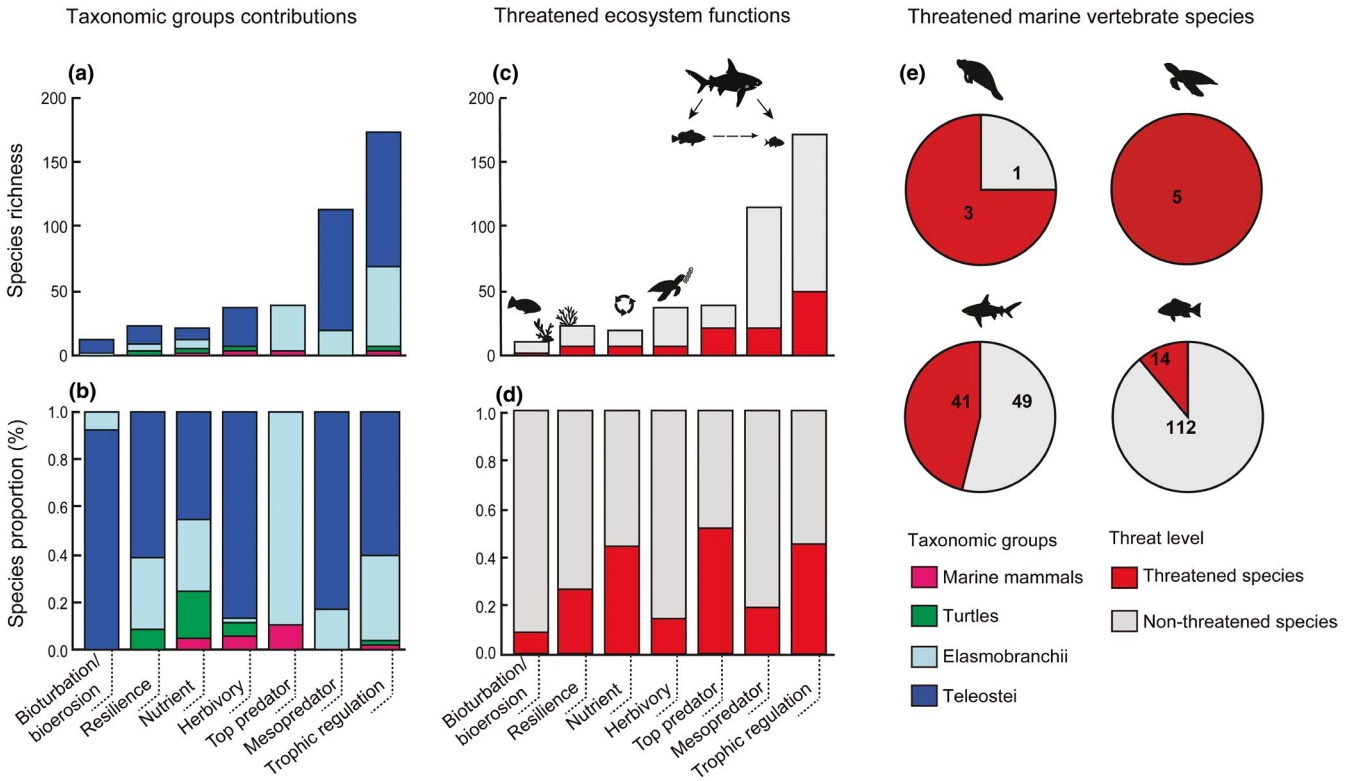

FIGURE 1 The contribution of taxonomic groups to the ecosystem functions identified and the ecosystem functions delivered by threatened (red) and non-threatened (grey) vertebrates in Atlantic Ocean reefs. (a, b) Richness and proportion of taxonomic groups delivering each ecosystem function (c, d) and the richness and proportion of threatened species (CR, EN and VU) associated with different each ecosystem functions. (e) The species richness (numbers in bold) and the proportion (circle colours) of each threatened taxonomic group

2.3.2 | Mapping functional richness, uniqueness and specialization in Atlantic Ocean reefs

For each grid cell, we calculated species richness as well as a set of metrics describing the functional structure at the assemblage level. We first calculated the functional richness (FRic) corresponding to the trait volume occupied by species co-occurring in each grid cell (Villéger et al., 2008). We then characterized the level of isolation of each species inside the functional space for each grid cell, which allows quantifying the level of species' uniqueness or redundancy at the assemblage level (Mouillot, Graham, et al., 2013; Pimiento, Leprieur, et al., 2020).

To do so, we calculated the mean functional uniqueness (FUn) per grid cell as follows. First, FUn was calculated based on Gower's distance as the mean distance between each species and the five nearest neighbouring species in the grid cell (see Pimiento, Leprieur, et al., 2020). Then, FUn was averaged across all species co-occurring in each grid cell. The mean functional uniqueness (or functional originality "FOri" sensu Mouillot, Graham, et al., 2013) increases as species contained in an assemblage share less traits with others. We also calculated the mean functional uniqueness considering the three, ten and fifteen nearest neighbouring species (see Figure S2). Last, we calculated the functional specialization (FSpe) for each grid cell (Mouillot, Graham, et al., 2013). FSpe was calculated as the mean distance of each species to the centroid of the functional space considering only species co-occurring in each grid cell, which allows distinguishing between assemblages dominated by species close to the centre of the trait space (displaying average trait combinations, i.e. generalist species) and those dominated by species near the edges of the trait space (displaying extreme trait combinations or specialist species; Mouillot, Graham, et al., 2013). The FUn and FSpe are therefore complementary in describing the functional structure of species assemblages (see Leitão et al., 2016).

2.3.3 | Simulating the effect of species extinctions on the loss of ecosystem functions

Ecosystem functions differ in their redundancy and in trait variation, which influence the effect of species loss on ecosystem functioning. To investigate the influence of future extinctions on the functional structure, we simulated extinctions by selectively removing species according to their IUCN status. First, we removed highly threatened species until reaching non-threatened ones (from Critically Endangered, to Endangered, Vulnerable and non-threatened species). We measured the loss in functional space (% FRic) due to the removal of threatened species (0%–100% of local species) at the regional scale. The proportion of functional space lost due to the simulated extinctions was obtained by calculating the functional richness after each simulated extinction. We calculated such

difference considering species representing "bioturbation/bioerosion," "herbivory pressure," "top predator" and "mesopredator" ecosystem functions for three different marine regions: the Caribbean, the Southwestern Atlantic and Eastern Atlantic (Floeter et al., 2008). These regions were used because low species richness for "bioturbation/bioerosion" and "herbivory pressure" ecosystem functions at the assemblage scale (grid cell) precluded the calculation of functional richness. We used a null model approach to randomly remove 100% of species from each community and contrast random species' loss to an ordered removal of 100% of species according to extinction vulnerability (IUCN categories). From one thousand simulated communities and their functional space loss, we extracted the first and fourth quantiles as well as the average null values of functional erosion. To test for the effect of species' removal on functional loss at the assemblage scale (each grid cell), we removed marine mesopredators (n = 119), across all assemblages because this group presents high species richness. We simulated the removal of mesopredator species until reaching species assigned to other functions at the community and calculated the proportion of functional loss. Then, to evaluate whether the potential extinctions of mesopredators may lead to a disproportionate decrease in functional richness (i.e. greater loss of functional richness than that expected by species richness alone), we used a null model that keeps constant the species richness in each assemblage (grid cell) and randomly removes from 1% to 100% of species 1,000 times, without considering their ecosystem functions. The "observed loss of functional richness" (I_{obs}) is compared to 1,000 simulated values (I_{sim}) (Gotelli & McCabe, 2002) by extracting the standard deviation (σ_{sim}) and the average ($\bar{I}_{sim}$), and subsequently by calculating a standardized effect size (SESn) as follow

$$SES_n = \frac{I_{obs} - \bar{I}_{sim}}{\sigma_{sim}}$$

A positive value indicates a greater decline in functional richness than that expected by randomly removing species from local assemblages. All analyses were performed using the R software version 3.4.4 (R Core Team, 2018).

3 | RESULTS

Our database comprises 224 vertebrate species, among bony fish, sharks, rays, sea turtles and mammals, associated with reef environments in the Atlantic Ocean. Ecosystem function information was available for 201 (89.7%) species (more details in 3.1.). Functional attributes cover 91.5% of the database. Maximum body mass and caudal fin shape classifications were the most complex attributes to compile because they were not available for all species. In addition, functional information on mammals was the most scarce among taxonomic groups. There are 63 threatened vertebrate species in Atlantic reefs, distributed in the Critically Endangered (n = 7), Endangered (n = 14) and Vulnerable (n = 42) threat categories (IUCN, 2019).

3.1 | The ecosystem functions of marine vertebrates in Atlantic Ocean reefs

Our literature search through 160 papers resulted in a list of seven ecosystem functions of reef vertebrates: 1. herbivory pressure, 2. nutrient transport and storage, 3. coral reef resilience, 4. bioturbation/bioerosion, 5. trophic regulation, 6. marine top predator and 7. marine mesopredator. This information was obtained for 201 of 224 species analysed here (see Table S1). Most species were included in "food web control" (Villéger et al., 2017) as trophic regulation (n = 175), followed by marine mesopredator (n = 119) and marine top predator (n = 32) (Figure 1). Just a few species were included in the bioturbation/bioerosion function (n = 12), which was mainly represented by Teleostei species (Figure 1a,b). Trophic regulation had the highest species richness as well as the greater number of threatened species (n = 50; 28.5%). Top predators had the highest proportion of threatened species (53.12%) as it includes 17 threatened sharks in a total of 32 sharks' species and three threatened large-bodied mammals in a total of four species (Figure 1c,d). Forty-one elasmobranch species found in Atlantic Ocean reefs are threatened with extinction (46%). The most threatened taxonomic group were sea turtles (n = 5; 100%) and mammals (n = 3; 75%) (Figure 1e).

3.2 | Linking threatened species, traits and ecosystem functions

The first four axes of the Principal Coordinate Analysis (PCoA) accounted for 88% of variation in regional functional space (PC1 = 38%, PC2 = 21%, PC3 = 17 and PC4 = 12%). The Tropical Northwestern Atlantic province, located in the southern Caribbean, had both the highest species richness (n = 134) and functional diversity (FRic = 0.94). The functional structure found in this province, and in the Tropical Southwestern Atlantic, corresponds to ~90% of the regional functional space—that of the totality of species considered in our study. In contrast, Benguela, located in southern Africa, presented the lower species richness (n = 31) and functional volume (40.6% of the regional functional space; see Figure S3). The distribution of threatened species in functional space (n = 63, 60.1% of the regional space) revealed that this set of vertebrates has a varied trait combination, occupying a large area including the extremes of the functional space (Figure 2a). The overlap of taxonomic groups in trait space suggests there is redundancy in the functions delivered by vertebrates in Atlantic Ocean reefs (Figure 2a). The largest overlap between taxonomic groups in PC2 and PC3 was represented by bony and elasmobranch reef fishes (30.94%), which also filled the largest functional volumes in regional trait space (53.1% and 29.3%, respectively). Sea turtles and marine mammals did not overlap in trait space, yet both groups overlapped mainly with bony fishes (1.76% for marine turtles in PC2 and PC3) (Figure 2a). Ecosystem functions overlap in functional space: trophic regulation encompasses top predators and mesopredators. When we consider the first two axes (PC1 and PC2), herbivory pressure is associated

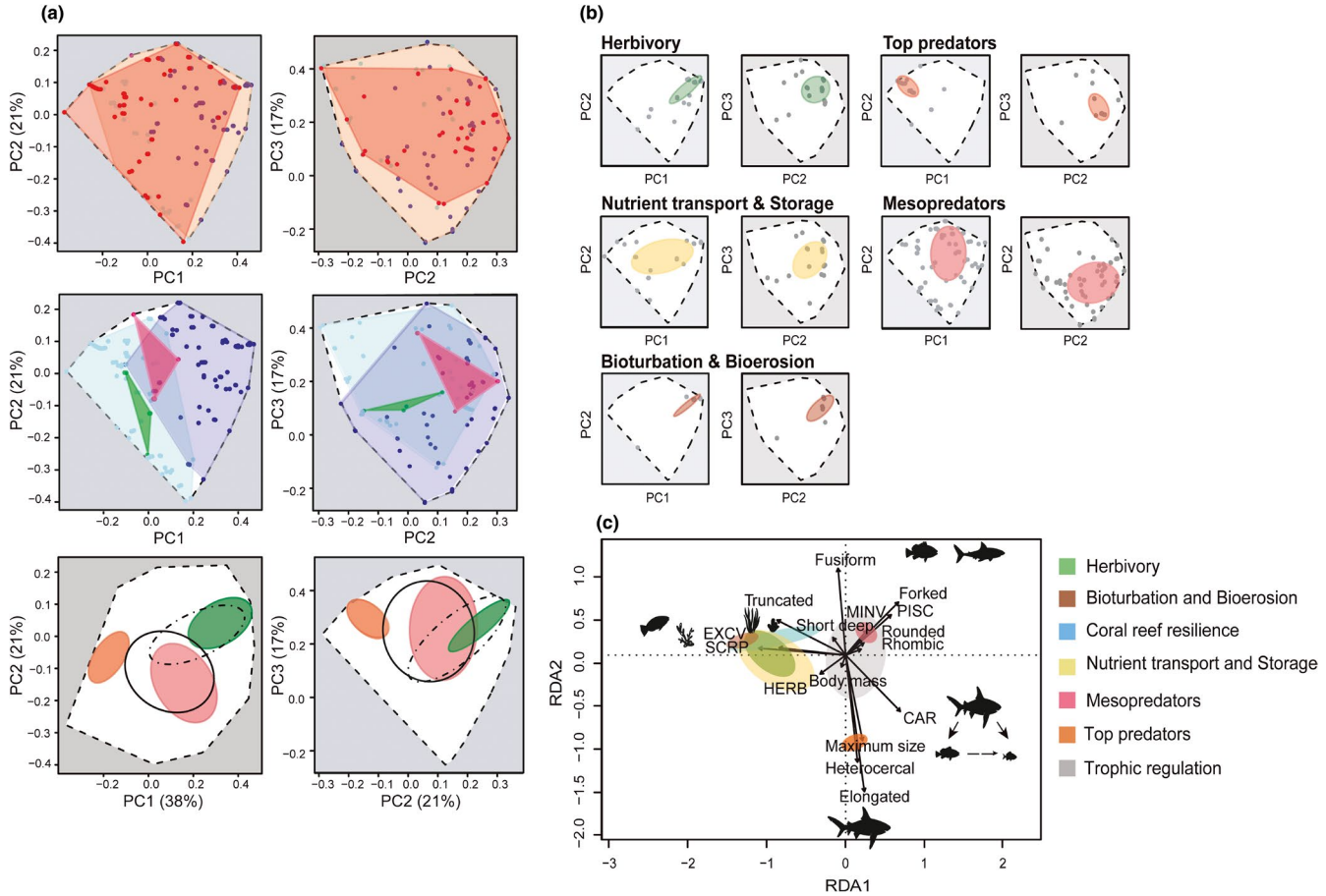

FIGURE 2 The functional space filled by marine vertebrates in Atlantic Ocean reefs (a), the ecosystem functions mapped in functional trait space (b) and the relationship between traits and ecosystem functions revealed through a Redundancy Analysis (RDA) (c). (a) TOP: the red polygon represents the volume filled by threatened species (60.1%) and the light-orange polygon represents non-threatened species (92.5%) relative to the regional functional space (dashed line). CENTER: the volume filled by different taxonomic groups is shown in different coloured polygons: mammals (dark pink), sea turtles (green, 0.0156%), Elasmobranchii (light blue, 29.3%) and Teleostei (dark blue, 53.1%). BOTTOM: ecosystem functions of vertebrates are mapped into functional space: "Herbivory" (light green), "Top predators" (orange) and "Mesopredators" (pink). The solid line ellipse represents "Trophic regulation" and encompasses top predators, mesopredators and herbivores. The dotted ellipse represents "Coral reef resilience"; (b) the centroid of traits associated with ecosystem functions mapped in functional space; (c) RDA plot of the relationship between the trait categories and the ecosystem functions performed by vertebrates in Atlantic reefs

with coral reef resilience. When the second and third PCoA axes are taken into account, herbivory encompasses trophic regulation and mesopredator species (Figure 2a). Despite the (low to intermediate) functional uniqueness patterns identified at the regional scale, different ecosystem functions were mapped in different areas of the functional space (Figure 2b). Indeed, the Redundancy Analysis has revealed that different functions are performed by species with specific sets of traits (ANOVA = p <.001; R^2 = .615). Species with herbivorous, scraper and excavator feeding modes, truncated caudal fin and short deep body shape were mainly related to coral reef resilience, nutrient transport and storage and bioturbation/bioerosion functions. Mesopredators, top predators and trophic regulation functions were performed mainly by carnivorous species with trait combinations as (1) large-bodied species with elongated body shapes and heterocercal caudal fin and (2) piscivorous species with forked caudal fin, respectively (Figure 2c). For a sensitivity analyses excluding species with no caudal fin classifications, see Figure S4).

3.3 | Functional diversity across Atlantic Ocean reefs

Within the Atlantic Ocean, the Caribbean region (Warm Temperate Northwestern Atlantic and Tropical Northwestern Atlantic provinces) concentrates the greater vertebrate species richness (Total species richness = 230). However, within this region, large differences in species richness per grid cell are observed, with greater richness observed in the Greater Antilles than in the Gulf of Mexico (with the exception of the Flower Garden Banks). The Southwestern Atlantic (Tropical and Warm Temperate Southwestern Atlantic provinces) also presented high species richness at the grid scale (80–100 species). In contrast, Eastern Atlantic reefs had the lowest vertebrate richness, with most assemblages being composed of <60 species (Figure 3a). Functional richness (FRic) showed similar spatial variation as species richness (Figure 3b), these two diversity facets being positively and strongly associated (Linear regression:

R^2 = .87, p < .01, see Figure S5). Functional uniqueness displayed greater values in one grid cell of the Caribbean region but also in one cell of the Eastern Atlantic (e.g. Benguela). FUn and species richness were found to be negatively and strongly associated (R^2 = .74, p < .01; Figure S5), FUn showing the lowest values (i.e. lower level of functional redundancy) in species-poor assemblages (Figure 3c). Also, functional specialization showed a similar pattern, with higher value for one assemblage in the North-Eastern Caribbean region (Figure 3d). FSpe and species richness were also found to be negatively related (R^2 = .63, p < .01; Figure S5).

3.4 | Influence of simulated extinctions on ecosystem functions

At the regional scale, the simulated removal of threatened and non-threatened vertebrate species associated with specific ecosystem functions did not differ from the losses expected at random (Figure 4a–c). The only exception was for mesopredators, whose simulated extinction shrunk 40% of the regional functional space. In this case, the loss of mesopredators followed by the random removal of vertebrate species was greater than expected by chance (Figure 4d). At the scale of marine regions (Figure S6a–l), the removal of mesopredators also significantly impacts the functional space of the Caribbean and Southwestern Atlantic regions (Figure S6j,k). In the Eastern Atlantic, herbivorous' species removal compromises almost 20% of functional richness (Figure S6f). At the assemblage scale, Atlantic reefs might be largely compromised by the loss of mesopredators species, which in certain communities reaches up to 90% of functional loss. The largest proportion of species loss in reef communities through the removal of mesopredators was identified for the Caribbean (60%), followed by the Brazilian (50%) and the western African coasts (45%) (Figure 5a). The greatest impacts in functional space following the removal of mesopredators occurred in southern Caribbean reef communities (94%) and in the southern part of the Southwestern Atlantic (70%–90%), followed by northern Africa (75%–90% of functional loss; Figure 5b). The null model has revealed that the observed mesopredators' functional loss is higher than expected at random mainly for assemblages at the Eastern Atlantic, but it does not differ from random expectations in almost all assemblages of Caribbean reefs (Figure 5c). Sites with greater mesopredator species richness have higher functional redundancy—-i.e. lower functional losses (Figure S7).

4 | DISCUSSION

We have found that it is the loss of mesopredator species that will severely compromise the functional structure of Atlantic Ocean reefs, from regional to local scales. This is possibly an outcome of the variety of traits found in mesopredators, which imply a broad distribution in functional space, high functional richness and greater functional losses when extinct. Despite the recognized importance of large-bodied sharks as top predators in marine ecosystems (Hammerschlag et al., 2019; Heithaus et al., 2008), their (simulated) extinction did not affect the functional diversity of Atlantic reef assemblages as predicted. At the global scale, mammals, sharks, rays and bony fishes together occupy most of the functional space of the marine megafauna (Pimiento, Leprieur, et al., 2020). At this scale, the potential extinction of threatened elasmobranchs will cause the most severe changes in functional richness and uniqueness (Pimiento, Leprieur, et al., 2020).

Our analysis revealed that the considered traits were consistently associated with particular ecosystem functions and that marine mammals, sea turtles and fish species in Atlantic Ocean reefs shared numerous functions. The importance of these four taxonomic groups and their functions in reef ecosystems have been reported and categorized (Brandl et al., 2019; Hammerschlag et al., 2019; Luiz et al., 2019; Pimiento, Leprieur, et al., 2020; Tavares et al., 2019; Villéger et al., 2017), but there have been few attempts to identify similarities in functions delivered by species belonging to such distant lineages, in a cross-taxa approach (but see Pimiento, Leprieur, et al., 2020).

When we simulated the loss of threatened vertebrate species (n = 63; 28.12%), we found that such loss may compromise the regional functional space (60.1%). Most of these threatened species share a macrocarnivore diet and large body sizes, which have been investigated in previous studies as predictors of extinction risk for fish and marine mammal species (Bender et al., 2013; Ceretta et al., 2020; Dulvy & Reynolds, 2002; Dulvy et al., 2003). Sharks are the majority of top predator species in Atlantic reefs (87.5%) and are largely threatened (46%). In the Atlantic, these species suffer from impacts as bycatch (Oliver et al., 2015), trade and food consumption (Barreto et al., 2017) and overexploitation (Luiz & Edwards, 2011). Further, sharks share life-history traits, as slow growth and late maturity, which increase their vulnerability and hamper stock recovery (Dulvy et al., 2014; Stevens et al., 2000). Despite the important role of sharks on ecosystems, the redundancy among top predators is questionable since most shark species are now considered mesopredators given reductions of their size and body mass (Roff et al., 2016). This result reinforces threats to marine mesopredators since the scarcity of top predators makes this functional group the next to be depleted from marine food webs (Ferretti et al., 2010; Myers et al., 2007; Roff et al., 2016).

Contrary to our hypothesis, our results show that despite the low herbivore species richness (n = 36), trait diversity in functional space (and functional uniqueness) ensures herbivory in the Caribbean and Southwestern Atlantic. In these reefs, herbivory is mainly performed by bony fishes through diverse feeding modes as browsing, excavating or scraping on the reef substrate (Ferreira & Gonçalves, 2006; Francini-Filho et al., 2010; Mantyka & Bellwood, 2007). Yet, different herbivorous species, as bony fishes, marine turtles and mammals may target distinct algal resources (Cardona et al., 2020; Castelblanco-Martínez et al., 2009; Tebbett et al., 2020). For example, the herbivory pressure exerted by a single *Chelonia mydas* equals many fish individuals (Goatley et al., 2012), and green turtles have a major contribution in sheltered reefs

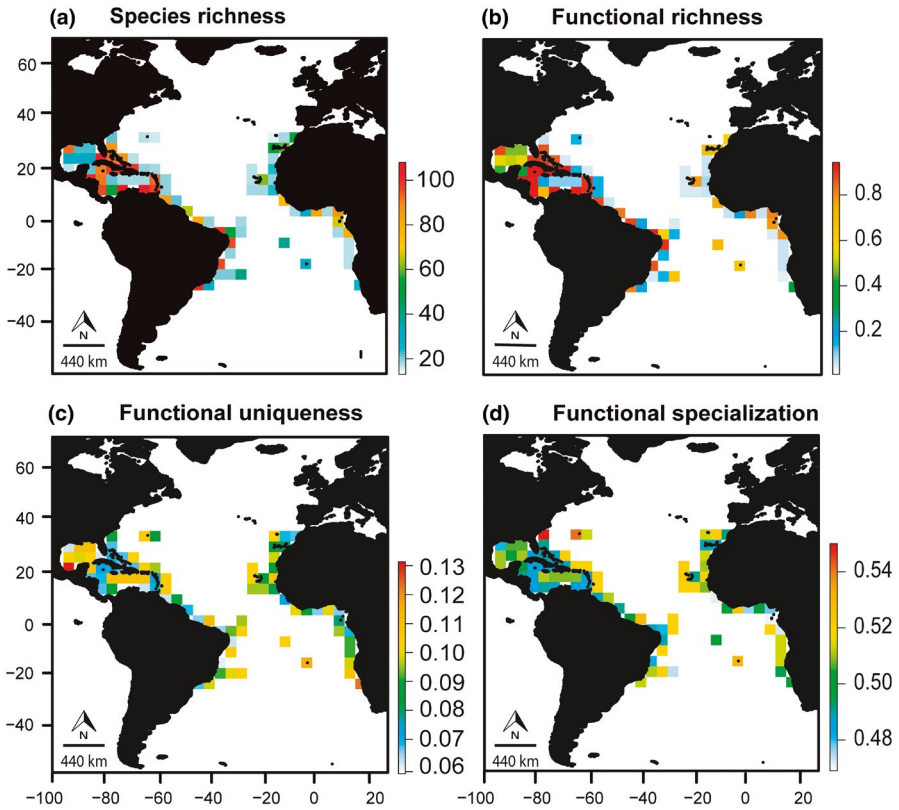

FIGURE 3 Spatial patterns of vertebrate diversity in Atlantic Ocean reefs (a) Total species richness; (b) Functional richness (FRic); (c) Functional uniqueness as a measure of functional redundancy; (d) Functional specialization considering the five closest species in functional space in each assemblage

with low rugosity, low coral cover and high algal cover (Cardona et al., 2020). Unfortunately, this essential reef function delivered by threatened herbivorous reptiles and mammals, as *Chelonia mydas* and *Trichechus* spp., is at global risk (Atwood et al., 2020). Thus, functional complementarity is needed to maintain ecosystem functioning (Cardona et al., 2020).

As expected, being the centre of marine biodiversity in the Atlantic Ocean (Bellwood et al., 2004; Floeter et al., 2008), the Caribbean is a "hot spot" of reef vertebrate species richness and functional richness. Such species richness pattern has been observed for several marine taxonomic groups in the Atlantic Ocean (McWilliam et al., 2018; Miloslavich et al., 2010; Mouillot et al., 2014; Polanco et al., 2020; Roberts et al., 2002; Tittensor et al., 2010). In the Caribbean, vertebrate species richness ensures the maintenance of certain ecosystem functions, as for top predators and herbivory, corroborating our hypothesis. Also, as the second centre of diversity in the Atlantic—being considered a regional hotspot accountable for 94% of the Southwestern Atlantic reef fish species endemism (Moura, 2002; Pinheiro et al., 2018)—the Brazilian coast presented a high species richness. The values exhibited for the Brazilian reef fauna are slightly lower when compared to the Caribbean, but greater than that of the African coast. The high functional richness identified for reefs in the Caribbean and along the Brazilian coast is possibly an outcome of the taxonomic diversity of their assemblages. While species richness means functional redundancy (Fonseca & Ganade, 2001; Halpern & Floeter, 2008), it also means that functional vulnerability (Mouillot et al., 2014) and uniqueness could characterize these assemblages. Such uniqueness is possibly caused by the local presence of different taxonomic groups, which are expected to be more distinct physically and functionally (Hammerschlag et al., 2019).

Despite the similar patterns of functional uniqueness and specialization of vertebrates in Atlantic Ocean reefs, the loss of mesopredators will modify the functional structure of assemblages, especially those with lower species richness. The importance of mesopredators to reef functioning is well known (Roff et al., 2016). Their removal from reef ecosystems can alter not only patterns of nutrient cycling between reef habitats but also the behaviour of prey species (McCauley et al., 2012; Rizzari et al., 2014). Furthermore, there is evidence for limited redundancy between small sharks and bony fish based on maximum prey size and gape width analysis, suggesting the unique role of these reef sharks as mesopredators (Barley et al., 2020). In the Caribbean, the most diverse vertebrate reef assemblage in the Atlantic, changes in reefs have been associated with the absence of mesopredator species as groupers and sharks, caused by fishing pressure, habitat degradation and pollution (Cheung et al., 2010; Ward-Paige et al., 2010). In the Southwestern Atlantic coast, groupers have suffered marked population declines in recent decades (Bender et al., 2014; Zapelini et al., 2019). Overall, the rarity and limited distribution of sharks and large-bodied groupers to few reefs suggests that their ecological function as mesopredators may be compromised in the Brazilian province (Morais et al., 2017).

Reef ecosystems are home to a fascinating diversity of species, described in heterogeneous and admirable forms of life, yet the ecosystem functions delivered by distinct reef species are not fully understood. These habitats host approximately one third to

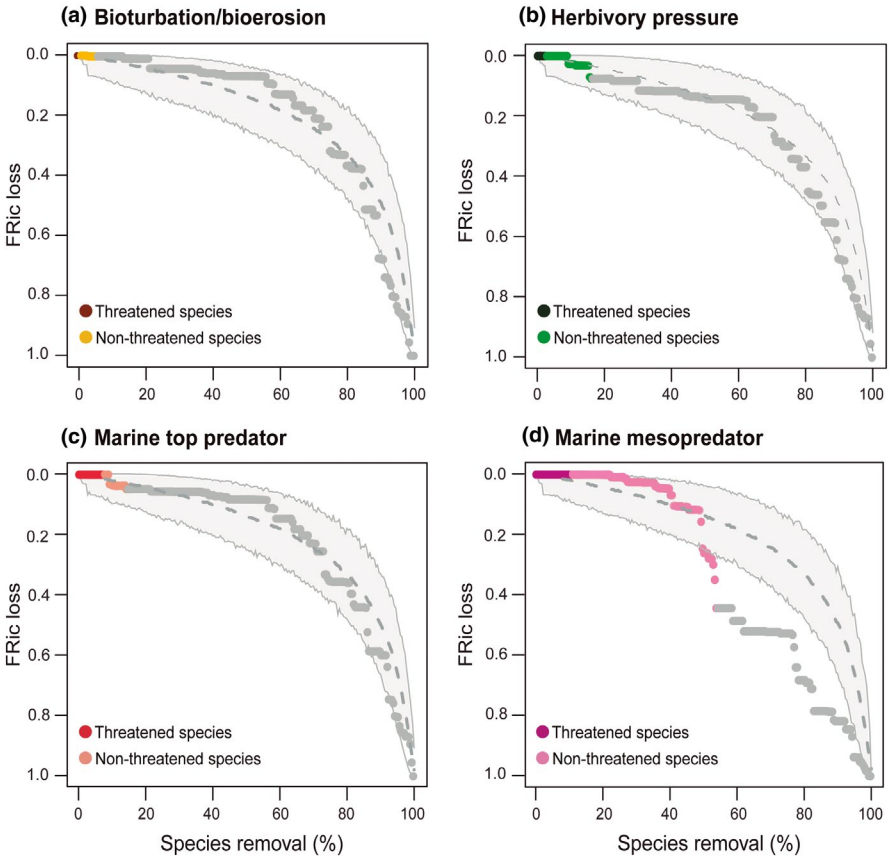

FIGURE 4 Functional richness loss in Atlantic Ocean reefs following the removal of threatened species within different ecosystem functions: (a) "Bioturbation/bioerosion"; (b) "Herbivory pressure"; (c) "Top predator" and (d) "Mesopredator". Grey points represent other species that do not perform these ecosystem functions in particular. Solid lines represent the 95% CI of the null model distribution, where species are randomly removed

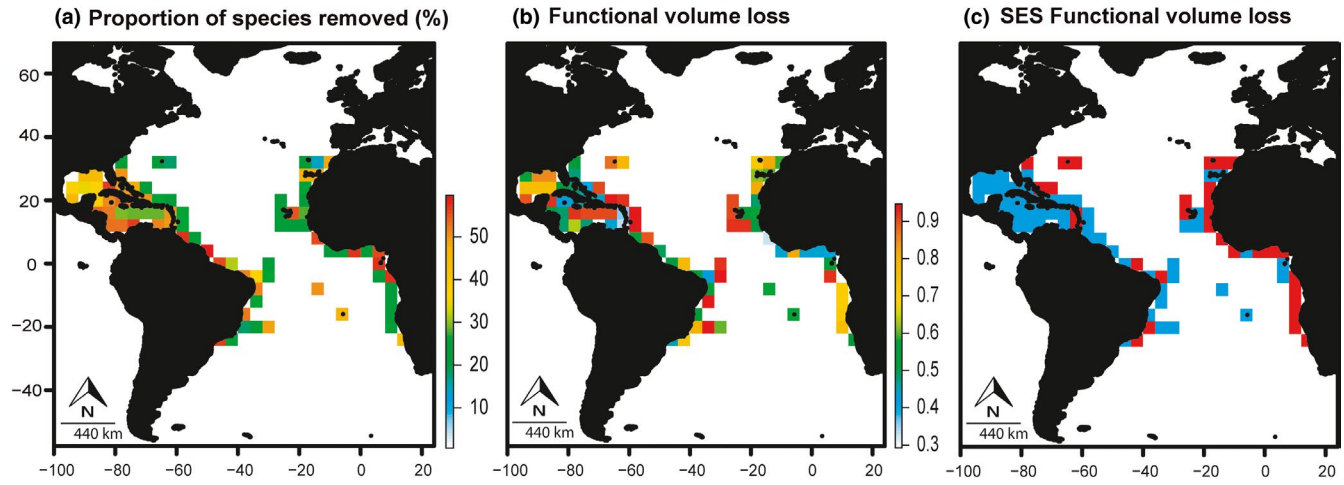

FIGURE 5 The effects of marine mesopredator loss in (a) the proportion of diversity loss in assemblages, (b) its functional loss (i.e. each grid cell represents an Atlantic Ocean reef vertebrate assemblage) and (c) the standardized-effect size (SES) of the null model for functional diversity loss. The colour gradient represents the proportion (%) and volume loss values (blue: low values; green to yellow: intermediate values; orange to red: high values). Red grid cells have functional richness loss greater than expected by chance (SES>0). Blue grid cells have functional richness loss greater than expected by chance (SES<0)

one quarter of all marine life, whereas one third of reef-building coral species are facing great extinction risk from local impacts and climate change (Carpenter et al., 2008; Fisher et al., 2015), compromising ecosystem functioning. The link between traits and ecosystem functions is essential to the management and conservation of reef species (Bellwood et al., 2019; Fonseca & Ganade, 2001; Pimiento, Leprieur, et al., 2020; Villéger et al., 2017). Our results reveal that functional traits can be properly associated with ecosystem functions and that distinct vertebrate lineages may deliver similar functions in reefs. The loss of mesopredators will affect one of the last resources of reefs, since top predator populations have already been greatly depleted (Worm et al., 2013). Then, the loss

of marine mesopredator function could severely compromise the structure and functioning of the majority of Atlantic Ocean reefs, reinforcing that these species deserve attention in future conservation planning. Our study does not provide a mechanistic understanding between traits and functions but evaluates whether some well-known functions in reef ecosystems can be related to particular or a set of traits. In that context, more experimental and fieldwork are needed to evaluate how species traits affect ecosystem functioning and to define the traits that are more strongly related to a "realized" function. As demonstrated in our analysis, studies on the ecosystem functions of marine species offer great opportunities to improve the roadmap for saving reefs from future degradation (Bellwood et al., 2019).

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CONFLICT OF INTEREST

The authors do not have a conflict of interest statement.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available at: https://github.com/luizawaechter/Atlantic-marine-vertebrate-species.

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